Egg Diameter Variation in Eastern North American Minnows (Pisces: Cyprinidae): Correlation with Vertebral Number, Habitat, and Spawning Behavior[1]

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ABSTRACT. **Data on mean diameters of mature, unspawned ova were obtained for 12 genera and 71 species of eastern North American cyprinids. Sizes ranged from approximately 0.7 mm for several species of *Notropis, Hybognathus hankinsoni,* and *Hybopsis aestivalis* to 2.0 mm for *Campostoma anomalum* (Reed 1958). Mean diameter is strongly conserved in several taxa including different subgenera of *Notropis.* In *Notropis* (*Luxilus*), mean diameter ranged from 1.24-1.41 mm, in *Notropis* (*Hydrophlox*) from 1.13-1.18 mm, and in *Notropis* (*Alburnops*) from 0.71-0.93 mm. *Notropis* (ss) and *Cyprinella* were exceptions, with both having a range of mean egg diameters that varied more than 0.50 mm. Mean vertebral counts were tabulated for 61 species. Regression and correlation analyses were performed on 20 non-*Notropis* species, 41 species of *Notropis,* and both combined. In all cases the slope of the regression line differed from zero at $P < 0.001$. Correlation coefficients (r) for the relationships of vertebral number to egg size were 0.930, 0.715, and 0.810, respectively. In addition, upland and montane species have larger eggs than lowland species; territorial and/or nesting species have larger eggs than those lacking these behaviors.**

OHIO J. SCI. 86 (3): 110-120, 1986

INTRODUCTION

Generally, it is well known that fish species with larger eggs tend to have more vertebrae (Lindsey and Ali 1971), spawn in cooler water (Ware 1977), and are more likely to build nests (Shine 1978) than related species with smaller eggs. Mean diameters of mature ova are reported regularly in life history studies of nearctic cyprinid fishes. They range from roughly 0.7 to 2.0 mm, or an increase in volume of 23X. Whereas egg size variation within a population is usually addressed, this obvious variation among many related species and its correlation with vertebral number, habitat, and spawning behavior have not been discussed adequately.

Vertebral number and egg diameter have never been compared directly in a study of a nearctic minnow, but several investigators have compared female size with egg diameter. Mathur and Ramsey (1974), Heins and Bresnick (1975), Heins and Clemmer (1976), and Heins et al. (1980) reported no correlation between the two, whereas Hoyt (1971) found a positive correlation for *Ericymba buccata.* Although cyprinids exhibit pleomerism, or a positive correlation between maximum body size and vertebral number (Lindsey 1975), it is obvious that in life history studies of single populations size will be more a function of age than differences in vertebral number. Comparisons among isolated populations of a species, or among several related species are necessary to discern a relationship.

Other than with female size, correlations are most often sought between egg diameter and environmental parameters, and are most common for commercially important marine species. Bagenal (1971) summarized available literature on both marine fishes with pelagic and demersal eggs as well as freshwater fishes. He concluded that seasonal change in egg size within a species is a biological rather than physical phenomenon, and is not dependent on seasonal changes in temperature or salinity. The most important factor affecting egg size in marine fishes appears to be seasonal availability of food (Bagenal 1971, Ware 1975, 1977). Among freshwater species, for which data are sparse, Bagenal (1971) found some geographic (e.g., *Oncorhynchus nerka, Cyprinus carpio*) and seasonal (e.g., *Salmo salar, Clupea harengus*) variation, which he attributed to food availability. However, the importance of detritus and other foods of terrestrial origin obscured any connection between primary production in streams and egg size. In a recent study, Heins and Baker (1985) found a positive correlation ($r = 0.825$) between egg diameter and mean annual runoff in an analysis of 16 Gulf coast populations of *Notropis venustus,* ranging from eastern Texas to northwestern Florida. Drift and detritus are probably correlated with runoff. This may account for one environmental factor in egg diameter variation. The influence of environmental and genetic factors on egg size is unknown.

The present study relies heavily on published records. It summarizes literature for 52 species (including 30 species of *Notropis*) in 12 genera of eastern cyprinids, presents new data for 19 additional species of *Notropis,* and duplicates measurements for another 20 species. Its purpose is to demonstrate the correlation of egg diameter with three parameters: mean vertebral count, habitat, and spawning behavior. The interplay among these factors is not generally appreciated in the literature on cyprinid systematics and life histories, but may be of some

[1]Manuscript received 16 October 1985 and in revised form 25 March 1986 (#85-49).

importance in formulating ideas on life history strategies and evolutionary trends.

METHODS AND MATERIALS

SOURCES OF SPECIMENS FOR ANALYSES. Specimens used for egg diameter measurements were obtained from the Ohio State Museum of Zoology (OSUM) collections, and are listed in Appendix I. Specimens used for vertebral counts were obtained predominantly from OSUM; some were also received from the University of Michigan Museum of Zoology (UMMZ) and Cornell University (CU). A list of these can be obtained on request. In cases where both were published, mean vertebral counts for the entire range of a species were used rather than counts for a local area. No attempt was made to match samples used for egg and vertebral studies.

RATIONALE FOR ESTIMATES OF MATURE EGG DIAMETER. Ripe females were opened, and mature, deep yellow eggs were removed from the posterior ovary. Ten eggs per female were measured with an ocular micrometer mounted on a Wild dissecting scope. Measurements on eggs from at least three females per species were desired, but not always obtained. Total egg counts were not made. In most cases the standard deviations (SD) of egg diameter measurements were well under 0.10; the 95% confidence intervals (CI) were in the range of ± 0.02-0.03mm. The largest variation occurred in *Notropis rubellus* (SD = 0.130, 95% CI = 1.08-1.14 mm) and *N. coccogenis* (SD = 0.132, 95% CI = 1.26-1.36 mm).

A mean value for mature egg diameter was necessary for the regression and correlation analyses and for analysis of variance (ANOVA). This was obtained by averaging all literature values and direct measurements for each species, regardless of the number of females in each sample. For species in which ranges, but not means, were published, the average of the range was used.

Six literature citations in Table I report a wide range of mature egg diameters for a single species. Each of these deserves comment. Mathur and Ramsey (1974) classified mature ova for *Notropis baileyi* in two ways. To estimate the number of clutches per spawning season, mature ova were given a range of 0.65 to 1.66 mm, with few larger than 1.40 mm. The second method involved the measurement of 10 to 20 of the largest ova in each ovary. This yielded a mean diameter that peaked in May at 1.15 mm. I used the latter for the average mean diameter for *N. baileyi.* Becker (1983) similarly estimated the diameters of mature ova from *N. anogenus* (0.7-1.3 mm for a single female) and *N. heterodon* (0.8-1.2 mm for three females). For this study, I took the midpoint of each range as an estimate of the mature mean diameter for *N. anogenus* and *N. heterodon.* There are other data available for both species, however. Starnes and Starnes (1981) reported an egg diameter range of 0.82 to 1.36 mm for *Phoxinus cumberlandensis.* They removed individual eggs from the entire ovary and estimated mature ova by color. Although this is a broad interpretation of what constitutes mature ova, I took the value of 1.09 mm as an estimate of the mean diameter of mature ova ready to be spawned. Jenkins and Burkhead (1984) reported a range of 0.8 to 1.4 mm for the eggs of *Hybopsis monacha.* Jenkins (pers. comm.) suggested that some females may have been in a rest interval between spawns, in accordance with their fractional spawning behavior, and perhaps lacked fully developed ova. The value of 1.10 mm is probably a low estimate for the mean diameter of mature ova for *H. monacha,* as is the average value for *P. cumberlandensis.* Finally, Brown and Hammer (1970) reported a range of 1.29 to 1.67 mm in the diameters of mature ova from *Couesius plumbeus.* Their data show a skewed distribution for May, 1967, with a mean value of 1.48 mm. This value was used in the present study.

With three exceptions, values in Table I were taken from preserved specimens. For *N. rubellus* and *Campostoma anomalum,* Reed (1958) placed eggs from fresh specimens in water prior to measurement. The

TABLE 1

Egg diameters, vertebral counts, habitat, and spawning behavior for some eastern North American cyprinids

Name	Female sample size	Egg diameter (mm)	Source	Average mean diameter (mm)	Mean vertebral count	Source	Habitat	Spawning behavior
Campostoma								
anomalum	1	1.3-1.5	Becker 1983	1.7	41.5	Present Study	U-M**	3***
	*	2.0	Reed 1958					
oligolepis	*	1.4	Becker 1983	1.4	*		U-M	3
Couesius								
plumbeus	*	1.29-1.67	Brown & Hammer 1970	1.48	40.5	Scott & Crossman 1973	L	2
	3	1.6	Becker 1983					
Ericymba								
buccata	107	0.75	Hoyt 1971	0.78	34.7	Present Study	L-U	1
	20	0.78	Wallace 1973					
	6	0.82	Present Study					
Hybognathus								
hankinsoni	1	0.7-0.8	Becker 1983	0.75	36.5	Scott & Crossman 1973	L	1
Hybopsis								
aestivalis	2	0.7-0.9	Becker 1983	0.80	36.3	Jenkins & Lachner 1971	L-U	1
amblops	3	0.96	Present Study	0.96	36.61	Clemmer & Suttkus 1971	L-U	1
monacha	5	0.8-1.4	Jenkins & Burkhead 1984	1.1	42.0	Jenkins & Lachner 1971	L-U	3
storeriana	3	1.3-1.5	Becker 1983	1.4	39.42	Jenkins & Lachner 1971	L-U	1
Notemigonus								
crysoleucas	2	0.84-1.10	Becker 1983	1.02	37.75	Scott & Crossman 1973	L-U	1
	*	1.2	Keast & Eadie 1984					
	3	0.90	Present Study					
Phenacobius								
mirabilis	2	1.25-1.30	Becker 1983	1.28	38.5	Present Study	L-U	*

TABLE 1 (continued)

Name	Female sample size	Egg diameter (mm)	Source	Average mean diameter (mm)	Mean vertebral count	Source	Habitat	Spawning behavior
Phoxinus								
cumberlandensis	*	1.82-1.36	Starnes & Starnes 1981	1.09	39.2	Starnes & Starnes 1978	U-M	2
eos	2	0.9-1.0	Becker 1983	0.95	36.7	Scott & Crossman 1973	L-U	2
erythrogaster	4	1.25	Becker 1983	1.15	37.0	Present Study	U-M	2
	40	1.05	Settles & Hoyt 1978					
neogaeus	1	1.0-1.1	Becker 1983	1.05	38.0	Scott & Crossman 1973	L-U	1
Pimephales								
notatus	3	1.0-1.2	Becker 1983	1.06	37.5	Scott & Crossman 1973	L-U	3
	*	0.95-1.0	Keast & Eadie 1984					
promelas	1	1.0	Becker 1983	1.0	36.6	Scott & Crossman 1973	L-U	3
vigilax	3	1.0-1.2	Becker 1983	1.10	37.7	Present Study	L-U	3
Rhinichthys								
atratulus	*	1.6	Dobie et al 1956	1.5	39.5	Present Study	U-M	3
	*	1.5	Noble 1964					
	2	1.4	Becker 1983					
Rhinichthys								
cataractae	2	1.5-1.7	Becker 1983	1.6	40.4	Present Study	U-M	3
Semotilus								
atromaculatus	2	1.4-1.7	Becker 1983	1.55	42.0	Scott & Crossman 1973	U-M	3
corporalis	*	2.16	Reed 1971	*	42.7	Scott & Crossman 1973	U-M	3
margarita	2	1.3-1.4	Becker 1983	1.35	39.3	Scott & Crossman 1973	L-U	2
Notropis								
Alburnops								
blennius	4	0.81-0.94	Becker 1983	0.78	36.4	Suttkus & Clemmer 1968	L	1
	5	0.68	Present Study					
chalybaeus	1	0.7-0.8	Becker 1983	0.71	34.94	Swift 1970	L	1
	3	0.67	Present Study					
dorsalis	2	0.9-1.0	Becker 1983	0.91	36.0	Present Study	L-U	1
	3	0.87	Present Study					
longirostris	70	0.90	Heins & Clemmer 1976	0.90	35.0	Present Study	L	1
N. sp. (cf *longirostris*)	18	0.80	Heins et al 1980	0.80	*		L	*
petersoni	2	0.93	Present Study	0.93	35.72	Swift 1970	L	*
procne	3	0.85	Present Study	0.85	34.9	Snelson 1971	L-U	*
stramineus	10	0.83-0.95	Tanyolac 1973	0.81	36.0	Present Study	L-U	1
	2	0.80	Becker 1983					
	94	0.75	Summerfelt & Minckley 1969					
	8	0.79	Present Study					
texanus	1	0.80	Becker 1983	0.82	36.18	Swift 1970	L	1
	3	0.84	Present Study					
Notropis								
Cyprinella								
callitaenia	*	1.2	Wallace & Ramsey 1981	1.2	39.0	Bailey & Gibbs 1956	L-U	3
galacturus	40	ca 1.6	Outten 1958	ca 1.6	40.5	Present Study	L-U	3
lutrensis	40	0.90	Farringer et al 1979	0.90	34.9	Present Study	L-U	3
pyrrhomelas	3	1.39	Present Study	1.39	37.8	Present Study	L-U	3
Hydrophlox								
baileyi	10	0.66-1.65	Mathur & Ramsey	1.15	37.40	Swift 1970	L-U	*
chlorocephalus	6	1.13	Present Study	1.13	38.4	Present Study	L-U	*
leuciodus	4	1.13	Present Study	1.13	39.21	Swift 1970	U-M	*
nubilus	1	1.0-1.2	Becker 1983	1.18	37.6	Present Study	U-M	2
	9	1.25	Present Study					

TABLE 1 (continued)

Name	Female sample size	Egg diameter (mm)	Source	Average mean diameter (mm)	Mean vertebral count	Source	Habitat	Spawning behavior
rubellus	9	1.0-1.2	Becker 1983	1.14	40.1	Swift 1970	U-M	2
	*	1.2	Reed 1958					
	9	1.11	Present Study					
rubricroceus	42	ca 1.6	Outten 1957	ca 1.6	39.53	Swift 1970	M	*
Luxilus								
chrysocephalus	3	1.24	Present Study	1.24	39.50	Gilbert 1964	L-U	3
coccogenis	50	ca 1.5	Outten 1957	1.41	41.12	Gilbert 1964	U-M	3
	3	1.31	Present Study					
cornutus	2	1.2-1.3	Becker 1983	1.25	40.08	Gilbert 1964	U-M	3
pilsbryi	3	1.40	Present Study	1.40	39.78	Gilbert 1964	U-M	3
zonatus	1	1.37	Present Study	1.37	39.95	Gilbert 1964	U-M	3
Lythrurus								
ardens	6	0.92	Present Study	0.92	38.9	Snelson 1972	L-U	2
roseipinnis	70	0.77	Heins & Bresnick 1977	0.77	36.3	Snelson 1972	L	2
umbratilis	2	0.6-0.75	Becker 1983	0.73	36.7	Present Study	L	2
	32	0.81	Matthews & Heins 1984					
	6	0.78	Present Study					
Notropis (ss)								
atherinoides	2	0.8-0.9	Becker 1983	0.85	39.4	Resh et al 1976	L	1
	3	0.85	Present Study					
photogenis	10	1.02	Present Study	1.02	40.2	Present Study	L-U	1
scepticus	22	0.8-1.1	Harrell & Cloutman 1978	0.95	36.8	Present Study	L-U	*
stilbius	4	0.77	Present Study	0.77	37.6	Present Study	L-U	*
telescopus	12	1.29	Present Study	1.29	38.29	Gilbert 1969	U-M	*
Opsopoeodus								
emiliae	3	0.9-1.1	Becker 1983	0.93	37.90	Gilbert & Bailey 1972	L-U	*
Pteronotropis								
hypselopterus	1	0.98	Present Study	0.98	36.3	Present Study	L	*
Others:								
Notropis								
amnis	1	0.80	Present Study	0.80	35.8	Present Study	L	*
anogenus	1	0.7-1.3	Becker 1983	1.01	*		L-U	*
	2	1.01	Present Study					
bifrenatus	1	0.81	Harrington 1984	0.81	*		L-U	*
boops	20	1.10	Lehtinen & Echelle 1979	1.07	36.5	Present Study	L-U	*
	3	1.04	Present Study					
buchanani	4	0.64	Present Study	0.64	35.0	Present Study	L	1
chihuahua	10	0.7-1.0	Burr & Mayden 1981	0.85	35.2	Burr & Mayden 1981	L-U	*
cummingsae	2	0.83	Present Study	0.83	*		L	*
greenei	3	1.11	Present Study	1.11	36.7	Present Study	L-U	*
harperi	*	1.1-1.2	Marshall 1947	1.15	36.9	Jenkins & Lachner 1971	L-U	*
heterodon	3	0.8-1.2	Becker 1983	0.94	37.0	Present Study	L-U	*
	*	0.9	Keast & Eadie 1984					
	2	0.90	Present Study					
heterolepis	2	0.8-0.9	Becker 1983	0.80	36.0	Present Study	L-U	*
	4	0.74	Present Study					
hudsonius	2	1.0-1.1	Becker 1983	0.95	38.1	Present Study	L	1
	2	0.83	Present Study					
N. sp. ("sawfin" shiner)	2	0.92	Present Study	0.92	*		L-U	*
volucellus	2	0.75-1.0	Becker 1983	0.90	36.7	Burr & Mayden 1981	L-U	*
	5	0.92	Present Study					

*No data available
**L = lowland habitat; L-U = lowland-upland; U-M = upland-montane; M = montane only. Modified from Jenkins et al 1972.
***1 = no specialized spawning behavior; 2 = moderately territorial and usually spawning over other species' nests; 3 = strongly territorial, crevice spawners, nest builders, or at least capable of occasionally making a nest (e.g. *Luxilus*).

value for *N. rubellus* was 1.2 mm, which is larger than other measurements for this species. The average diameter (2.0 mm) for *C. anomalum* is much larger than the range of 1.3 to 1.5 mm reported by Becker (1983). I averaged both values to obtain a mean diameter of 1.7 mm for this species. Reed (1971) reported an average value of 2.16 mm for water-hardened, but unfertilized eggs of *Semotilus corporalis.* I had no way of accurately estimating how much the diameter of eggs from this species increased after spawning; therefore, no average mean diameter is listed for *S. corporalis,* and it was not included in subsequent analyses.

Preliminary regressions of mean vertebral number on mean egg diameter indicated that the values for *H. monacha, Notropis galacturus, N. rubricroceus,* and *N. photogenis* were highly deviant. I eliminated *H. monacha* for the reasons outlined above, and also *N. galacturus* and *N. rubricroceus* since Outten's (1958) egg sizes for these two species were based on estimates. Other values for *Hydrophlox* indicate that the mean egg diameter for *N. rubricroceus* should be about 1.2 mm. I retained *N. photogenis* since egg diameters were measured from 10 females from four different localities. An extensive series of vertebral counts on this species were also done.

STATISTICAL ANALYSES. All statistical tests were performed with a Minitab statistical package (Minitab, Inc. 1983). Vertebral means were regressed as dependent variables on mean egg diameters. In addition, a correlation analysis was done on this data set. Egg diameters were compared to habitat and spawning behavior with one-way analysis of variance (ANOVA).

Jenkins et al. (1972) assigned most species used in the present study to habitat categories. Using their designations, I coded habitats on the following basis: 1, lowland only; 2, both lowland and upland; 3, upland only; 4, both upland and montane; 5, montane only. I modified designations where appropriate (e.g., Jenkins et al. (1972) assign *Notropis volucellus* to an upland habitat in the southern Appalachians, but I assigned it to the lowland-upland category based on its habitat throughout its entire range. Species not covered by Jenkins et al. (1972) were assigned habitats based on pertinent literature. Preliminary analysis showed no significant difference between groups 2 and 3; thus, these were lumped into a single lowland-upland group. Because *Notropis rubricroceus* was the sole member of group 5, this category was eliminated. Thus, the ANOVA compared lowland, lowland-upland, and upland-montane groups.

Spawning behaviors were classified into three groups for ANOVA. Species in group 1 were not territorial, nor did they spawn in the nests of other species. Species in group 2 usually used the nests of other species for spawning. Some of the species in this group were territorial, and some were not. Members of group 3 were strongly territorial. They were nest builders, crevice spawners (e.g., *Notropis (Cyprinella)* species), or at least capable of occasionally constructing a nest (e.g., *Notropis (Luxilus)* species). Of the original 71 species, only 48 could be placed in reproductive groups. Data on egg diameter, vertebral count, habitat, and spawning behavior were available for only 42 species.

RESULTS

A summary of egg diameters for 71 species and vertebral counts for 65 species is presented in Table 1. The number of females in Table 1 refers only to egg diameter data. No vertebral count data were available for six species: *Campostoma oligolepis, Notropis* sp. (cf. *N. longirostris*), *Notropis* sp. ("sawfin" shiner), *N. anogenus, N. bifrenatus,* and *N. cummingsae.* Taxonomic nomenclature follows Robins et al. (1980). Species of *Notropis* (sl) are organized into subgenera, with assignments following Swift (1970) for *Alburnops* and *Hydrophlox,* Snelson (1968, 1972) for *Notropis* (ss) and *Lythrurus,* respectively, Gibbs (1957) for *Cyprinella,* Gilbert (1964) for *Luxilus,* Gilbert and Bailey (1972) for *Opsopoeodus,* and Bailey and Suttkus (1952) for *Pteronotropis.* The remainder were placed in the "others" category. Among eastern genera no egg diameter data were found for *Nocomis, Dionda, Hemitremia, Codoma, Clinostomus,* and *Exoglossum.*

INTERSPECIFIC EGG DIAMETER VARIATION. Mean diameters measured during the present study ranged from 0.64 mm for *Notropis buchanani* to 1.39 mm for *N. pyrrhomelas.* In published accounts egg diameters ranged from about 0.7 mm for several species of *Notropis, Hybognathus hankinsoni,* and *Hybopsis aestivalis* (Becker 1983) to 2.0 mm for *Campostoma anomalum* (Reed 1958). Whereas some average diameters were calculated from dozens of specimens, in 27 of 71 species (38%) the average diameter was based on measurements from three or fewer females. When duplicate measurements existed for a species, results were generally in close agreement, and supported the interpretation that egg size is fairly constant within a species. Some exceptions are the values for *Campostoma anomalum* (1.3-1.5 mm, Becker 1983; 2.0 mm, Reed 1958); *Notemigonus crysoleucas* (0.90 mm, present study; 1.2 mm, Keast and Eadie 1984); *Notropis blennius* (0.68 mm, present study; 0.88 mm, Becker 1983); and *N. hudsonius* (0.83 mm, present study; 1.05 mm, Becker 1983).

Although sample sizes were small, two trends were evident within subgeneric groups of *Notropis* (sl). In *Lythrurus, Alburnops,* and especially *Luxilus* and *Hydrophlox,* there was relatively little variation in average mean egg diameters. In *Notropis* (ss) values ranged from 0.77 mm for *N. stilbius* to 1.29 mm for *N. telescopus. Notropis* (ss) is at present not well-defined, and the variation observed among its members may have been due to grouping more distantly related species. However, examination of the other four subgenera provided a potentially important evolutionary insight. Egg diameter is apparently rather conservative and varied little among several related species. In *Luxilus,* average mean diameters changed only 0.17 mm among five species. In *Hydrophlox,* exclusive of Outten's (1958) value for *N. rubricroceus* (approx. 1.6 mm), the range was even smaller (1.13 mm for *N. leuciodus* to 1.18 mm for *N. nubilus*). *Cyprinella* could be an exception to this generalization; however, data were available for only four of 26 species. Mean egg sizes for these four species were 0.90 mm for *N. lutrensis* (Fig. 3, Farringer et al. 1979), 1.2 mm for *N. callitaenia* (Wallace and Ramsey 1981), 1.39 mm for *N. pyrrhomelas* (present study), and 1.6 mm for *N. galacturus* (Outten 1958). The difference between *N. lutrensis* and *N. pyrrhomelas* is 0.50 mm. Values from other species of *Cyprinella* are clearly needed.

An ANOVA comparing the four subgenera with data from five or more species showed significant differences among them. The results are summarized in Table 2.

In the other genera, the (about 1.4 mm) value for *Campostoma anomalum* (Becker 1983) was lower than the measurement of 2.0 mm for *C. anomalum* (Reed 1958). Species placed in *Hybopsis* represent several separate evolutionary lines (Table 1). Clemmer (1971) concluded that *Notropis amnis* and *Hybopsis amblops* are related, and that their mean egg diameters are similar. *Hybopsis monacha* (0.8-1.4 mm) could fit within the range for *Cyprinella* (Jenkins and Burkhead 1984). Values for *Pimephales* fall close to 1.0 mm, as do those for *Phoxinus,* with the exception of the average of 1.25 mm for *P. erythrogaster* (Becker 1983). In the genus *Semotilus, S. margarita* has the smallest egg, *S. atromaculatus* is in the middle, and *S. corporalis* probably has the largest (Table 1). Thus, like subgenera of *Notropis,* egg size is conserved with relatively little variation in many genera. However, as mean egg diameter increases, more variation among species occurs, and this is evident for recorded values within a species.

TABLE 2
ANOVA Comparing mean egg diameters for four subgenera of Notropis *(SL)*

Group	N	Mean	Standard deviation	Source	Df	SS	MS	F-statistic
Alburnops	9	0.834	0.071					
Hydrophlox	5	1.140	0.021					
Luxilus	5	1.330	0.083					
Notropis (ss)	5	0.976	0.199					
				Factor	3	0.888	0.296	25.92*
				Error	20	0.228	0.012	
				Total	23	1.116		

*P ≤ 0.01

VERTEBRAL NUMBER AND EGG DIAMETER. Regression and correlation analyses were performed on the average mean egg diameters and mean vertebral counts for 61 species, after eliminating four species with outlying egg diameter values and six species lacking vertebral counts. Three regression and correlation analyses were performed: the first on non-*Notropis* species, the second on *Notropis,* and the third on all. There was a strong correlation between egg diameter (EGG DIAM) and vertebral count (VERT) that cut across species of different phyletic lines, habitats, and niches. The regression equation for non-*Notropis* species was: VERT = 31.2 + 6.02(EGG DIAM); 0.75 mm ≤ EGG DIAM ≤ 1.7 mm (N = 20; R^2 = 0.865, P < 0.001). The equation for *Notropis* was: VERT = 31.4 = 6.02(EGG DIAM); 0.64 mm ≤ EGG DIAM ≤ 1.41 mm (N = 41; R^2 = 0.511, P < 0.001). The equation for all species combined was: VERT = 31.4 + 5.88(EGG DIAM); 0.64 mm ≤ EGG DIAM ≤ 1.7 mm (N = 61; R^2 = 0.657, P < 0.001) (Fig. 1).

HABITAT AND REPRODUCTIVE BEHAVIOR. There is a general correlation between habitat and egg diameter. Montane and headwater species have large eggs, whereas large river, lacustrine, and lowland species have small eggs. Riverine and some upland species are intermediate. Species classified into one of three habitat groups (lowland, lowland-upland, and upland-montane Table 1) were compared with a one-way ANOVA (Table 3). Lowland species had a mean egg diameter of 0.86 mm (SD = 0.19; 0.64 ≤ EGG DIAM ≤ 1.48 mm; N = 16). Lowland-upland species had a mean value of 1.02 mm (SD = 0.18; 0.78 mm ≤ EGG DIAM ≤ 1.5 mm; N = 37), whereas upland-montane species had a mean of 1.36 mm (SD = 0.19; 1.09 mm ≤ EGG DIAM ≤ 1.7 mm; N = 16). The differences among the groups were significant at the 0.001 level (F = 31.39). With the exception of the value (1.48 mm) for *Couesius plumbeus,* all lowland species have egg diameters less than 1.0 mm. *Phoxinus cumberlandensis* had the smallest egg diameter (1.09 mm) in the upland-montane group. As previously noted, its mean is probably based on a low estimate. The lowland and upland-montane groups are nearly mutually exclusive, therefore, but a large lowland-upland group lies between them. Within subgenera of *Notropis* (sl), *N.* (*Lythrurus*) *ardens,* an upland species, has a larger egg (0.92 mm) than the lowland *N. umbratilis* (0.73 mm) or *N. roseipinnis* (0.77 mm). In *Notropis* (*Cyprinella*), *N. lutrensis,* a lowland species, has a mean egg diameter (0.90 mm) much smaller than the species (*N. galacturus, N. pyrrhomelas, N. callitaenia* found in upland habitats. All members of the upland-montane *Hydrophlox* and *Luxilus* have large eggs for *Notropis* (sl).

Whereas the correlation between habitat and egg diameter was not surprising, there was also a relationship between large egg size and nest building and/or territorial behavior (Table 4). A one-way ANOVA revealed significant differences among three groups: 1) non-territorial species having no specialized reproductive behavior (mean EGG DIAM = 0.87 mm; 0.64 mm ≤ EGG DIAM ≤ 1.05 mm; SD = 0.12; N = 19); 2) moderately territorial species usually spawning over the nests of other species (mean EGG

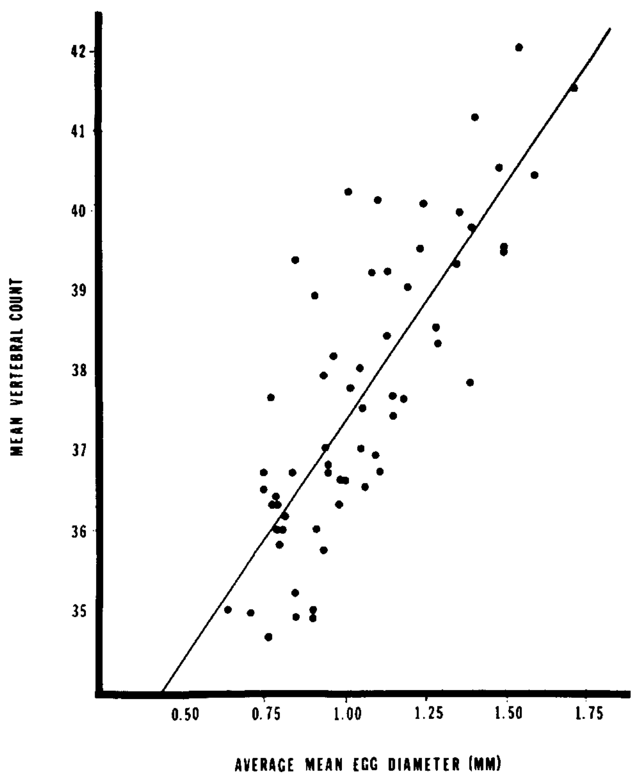

FIGURE 1. Relationship of mean vertebral count to average mean egg diameter for 61 species of eastern cyprinids: VERT = 31.4 + 5.88 (EGG DIAM).

TABLE 3
ANOVA Comparing habitat to mean egg diameter for 69 species of eastern cyprinds

Group	N	Mean	Standard deviation	Source	Df	SS	MS	F-statistic
Lowland	16	0.859	0.190					
Lowland-upland	37	1.017	0.180					
Upland-montane	16	1.360	0.193					
				Factor	2	2.157	1.079	31.39*
				Error	66	2.268	0.034	
				Total	68	4.425		

*P ≤ 0.01

DIAM = 1.07 mm; 0.73 mm ≤ EGG DIAM ≤ 1.48 mm; SD = 0.25; N = 9); and 3) strongly territorial and nesting species, including crevice spawners such as *Cyprinella* (mean EGG DIAM = 1.32 mm; 0.90 mm ≤ EGG DIAM ≤ 1.7 mm; SD = 0.22; N = 14).

Semotilus, Rhinichthys, and *Campostoma,* which are nest builders, had the largest egg diameters surveyed. *Rhinichthys* and *Campostoma* make a pit nest; *Semotilus* constructs a mound. Within *Notropis* (sl), *Luxilus* and *Cyprinella* have large sexually dimorphic males that defend territories. *Luxilus* species can make a pit nest during communal spawning (Raney 1940) or spawn over the nests of chubs. Members of *Cyprinella* are probably specialized crevice spawners (Wallace and Ramsey 1981, Jenkins and Burkhead 1984). Obvious exceptions to this generalization are species of *Pimephales,* who spawn in a nest which the male guards, and *Notropis* (*Cyprinella*) *lutrensis,* a crevice spawner. Both have eggs with a mean diameter of about 1.0 mm. At the other extreme, *Couesius* (1.48 mm) has a large egg but does not build a nest or guard its eggs. Although little is known of their biology, it seems likely that *Hybopsis storeriana* and species of *Hybopsis* (*Erimystax*) will prove to have large eggs, but not exhibit any territorial or nesting behavior.

In summary, the 29 species having a mean egg diameter less than 1.0 mm had a mean vertebral count of 36.36 (SD = 1.18). Thirteen are lowland dwellers, 16 are lowland-upland species. Sixteen belong to the group 1 spawning type, four to group 2, and only one to group 3. No spawning data were available on the remaining eight species. The 16 species with egg diameters of 1.0-1.2 mm had a mean vertebral count of 37.92 (SD = 1.19). Twelve are lowland-upland, and five are upland-montane. Based on the available data, three are group 1 spawners, four are in group 2, and three are in group 3. The 16 species with eggs larger than 1.2 mm had a mean vertebral count of 40.02 (SD = 1.33). One is lowland, five are lowland-upland, and 11 are upland-montane. Based on the available data, two are group 2 spawners, and 12 belong to group 3.

DISCUSSION

There are two problems that undoubtedly influenced the analyses done in the present study. The first is the small number of individuals used for many of the egg size measurements. Secondly, averaging egg diameter and vertebral number may obscure real intra- and interspecific differences by reducing variability and generating more positive correlation than actually exists. However, as a preliminary finding, such a high correlation is certainly interesting. Two hypotheses appear likely. One is that vertebral number is not causally linked to egg diameter. In fact, both may vary in response to one or more other parameters (e.g., temperature). Another is that vertebral number is dependent on egg diameter. The coefficient of determination of 0.657 found in the present study appears to favor the second.

The mechanisms controlling vertebral number in teleosts are undoubtedly complex (Fowler 1970, Lindsey and Arnason 1981). Hubbs (1922, 1926, 1934) envisioned two possibilities. In the first, the environment affects metabolic rate primarily by changes in temperature and/or salinity at the time of development. These in turn act in a linear fashion to directly influence vertebral number. Lower temperature delays the onset of segmentation

TABLE 4
ANOVA Comparing spawning behavior to egg diameter for 42 species of eastern cyprinids

Group	N	Mean	Standard deviaton	Source	Df	SS	MS	F-statistic
1*	19	0.870	0.125					
2	9	1.068	0.252					
3	14	1.317	0.225					
				Factor	2	1.735	0.867	23.04**
				Error	39	1.544	0.037	
				Total	41	3.279		

*Groups are defined in Table 1.
**P ≤ 0.01

until the absolute size is larger, and protracted development increases the number of vertebrae. Conversely, faster development at higher temperature terminates more rapidly the stage during which vertebrae form, thereby decreasing their numbers. Subsequent investigators (Taning 1952, Lindsey 1962, Ali and Lindsey 1974) demonstrated that the relationship to temperature is not linear. Lindsey and Arnason (1981) proposed a mathematical model, termed "atroposic", to account for the many, seemingly contradictory, responses of vertebral number to environmental influences.

The second mechanism (Hubbs 1926) is that the increased number of body segments is due to very large egg size (e.g., elasmobranchs). Hubbs referred to it as an obscure and indirect relation, that meets primarily developmental rather than environmental needs, and cannot be interpreted as a metabolic adaptation to the environment. Later, Hubbs (1941) and Hubbs and Hubbs (1945) suggested that the number of meristic elements is determined by the space available to them at the time of their formation. Kyle (1926) further noted that "... the smaller eggs yield the smaller larva and the smaller larva has the smaller number of vertebrae."

Lindsey and Ali (1971) critiqued the hypothesis that egg size controls vertebral number in teleosts, and concluded that morphogenic control of vertebral number does not reside in egg size. They acknowledged many instances in which larger eggs produce higher vertebral counts, when comparisons are made between genetically different units within the same species, genus, or family. But they also argued that among genetically similar fish the hypothesis that egg size controls vertebral number is not supported. Yet, by focusing narrowly on intrapopulation (often intraclutch) variation, while discounting interpopulation and interspecies evidence, a fundamental distinction can be obscured. Vertebral number for a population is represented by a modal value, and the variation around that mode. The present study supports a relation between egg diameter and the modal number of vertebrae, as approximated by the average. There is overwhelming evidence that environmental factors, especially temperature, induce variations around the mode. The question is: Can small changes in egg diameter also account for variations around the modal value, or a shift to a new modal value?

Data presented here could be helpful for predicting how much egg diameter variation contributes to the variation of vertebrae around a modal value. Vertebrae are integral units forming one at a time, whereas egg sizes are continuous variables. For the minnows studied, the slope of the regression line (5.88) predicts that a change of one vertebra occurs with a change in egg diameter of about 0.17 mm. For variations substantially smaller than this, little or no influence of egg size on vertebral number may occur. Other teleosts would be expected to have different slopes, but before concluding that a change in egg size has no effect on vertebral number, it is important to know how much of a change is necessary before one could reasonably expect to see a difference in vertebral number due to shifts in egg size alone. This kind of information can only come from interspecific comparisons.

The formation of vertebrae is a process dependent on space (or cell number, Lindsey and Arnason 1981), time, and rate. Space or cell number could be related to egg size, whereas the rate and duration of somite formation are dependent upon an interaction of environmental and genetic parameters. The importance of the latter two are predicted by the atroposic model (Lindsey and Arnason 1981). The importance of egg size in naturally occurring populations could be inferred from studies such as Heins and Baker (1985), who sampled populations of *Notropis venustus* from 16 Gulf slope drainages, and found significant differences in mean egg diameter among drainages. These differences were correlated with average annual runoff, suggesting that egg size variation within a species may be correlated with available food (Bagenal 1971). A follow-up study could be done on vertebral counts of fish of the same year-class as the eggs. If a high correlation was found between changes in egg diameter and vertebral number, an assessment of how much variation in egg diameter is necessary before correlated vertebral changes occur could be made. A study similar to Hubbs (1922) could also be done, in which one population is followed over two or more years, and correlations are done between egg diameter, vertebral number, runoff, and temperature. Alternatively, direct manipulation of eggs by increasing or decreasing egg volume in controlled laboratory experiments could also yield interesting results.

With the exception of *Pimephales*, the results presented here also support the contention of Shine (1978) that nesting species (e.g., *Semotilus, Rhinichthys, Campostoma*) have larger eggs than those lacking nesting and territorial behavior. The evolution of a large egg may be associated with cool temperatures, or with variability in stream conditions, or both. Lengthy developmental time may be the underlying factor promoting the evolution of nesting and territorial behavior. *Rhinichthys, Semotilus, Campostoma, Nocomis,* and *Exoglossum,* though not all related to each other, make nests. Other groups (e.g., *Luxilus, Hydrophlox, Notropis ardens, Phoxinus*) have moderate to large eggs and also use those nests. The similarity among these species appears to be the developmental requirements of an embryo growing on a large egg in a cool water, variable habitat, and taking a long time to hatch (5-10 days). The initial adaptive value of nest-building behavior was probably to protect the embryo from silt accumulation. Nest building, using nests of other species, or at least spawning in some silt-free substrate may be an inevitable consequence of living in cool upland or headwater streams. In this context, there is no reason why nest building could not develop in parallel in unrelated groups.

Nest-building behavior imparts a strong selective force for the male to become territorial. Territoriality may select for larger body size that in part could lead to still larger egg size. The "maleness" component of large body size can be separated from large size due to high vertebral numbers, which in this study was shown to be correlated with egg diameter. Cyprinids exhibit pleomerism, or a positive correlation between maximum body size and vertebral number (Lindsey 1975). In an unpublished study, the author examined this relationship in *Notropis.* There was a significant relationship ($r = 0.651$) for 76 species. For species in the subgenus *Notropis,* where females are larger than males, the correlation coefficient was 0.776. However, neither *Luxilus* nor *Cyprinella,* where males are larger, showed a significant correlation (r = 0.132 and 0.134, respectively). Thus, pleomerism is more correctly correlated with maximum female size. The extent to which pleomerism decreases, and males exceed females in length, gives an estimate of the selective pressure on the male to attain larger body size. Unfortunately, maximum female size is unknown for most species.

The most interesting exception to the correlation between large egg diameter and nesting behavior occurs in the genus *Pimephales.* Its members have the most complex reproductive behavior, and give more care to the fertilized eggs than any other American cyprinid. Yet, their eggs have a diameter of only 1.0-1.1 mm. Two explanations seem possible. The first is that *Pimephales* is related to species with smaller eggs, and within this evolutionary line *Pimephales* has increased egg diameter. The fact that they spawn in summer rather than in the spring may be indirect evidence in support of this hypothesis. The other explanation is that the nesting behavior may offer protection to the prolarvae following hatching (Shine 1978).

The present study indicated that the egg may be required by developmental processes, as reflected in vertebral number, to be roughly a certain size when mature. As species become smaller, they will inevitably become fractional spawners, that is, releasing mature eggs of a certain required size a few at a time, but over an extended period. Energy expenditure, as measured by a gonadosomatic index remains low (often below 10% of body wet weight) but investment over an entire season can be high (Gale and Buynak 1978). *Cyprinella* presents an interesting paradox. The fact that its members are fractional spawners implies an ancestral species with small body size. Yet, they are also territorial. Males of some *Cyprinella* species also attain very large body size. If all members of *Cyprinella* prove to be fractional spawners, it may well be that small body size is primitive within *Cyprinella,* and large body size is derived.

In summary, investigators studying the life histories of fishes should be aware that egg diameters and vertebral counts are correlated and vary little within many genera and subgenera. The origin of North American cyprinid genera predates the Pleistocene. The relative constancy of egg diameter and vertebral count over such an extended period involving many climatic shifts indicates that important aspects of larval ecology, breeding behavior, and habitat, which are all likely related to egg size, are probably also conserved. Thus, studies at the generic level may be more informative in trying to elucidate reproductive strategies than those of individual species.

Investigators seeking evolutionary characters should be impressed by the interplay among hard and solf anatomical features (e.g., vertebrae and egg diameter) and behavior. Because species evolve as complex organisms, changes in vertebral number, which are used as a standard taxonomic tool, should be viewed as part of a larger scheme implying correlated changes in other quantifiable characters. Careful documentation of these will lead to a deeper understanding of their rate of change and adaptive significance.

ACKNOWLEDGMENTS. I thank Ted M. Cavender (OSUM), R. R. Miller (UMMZ) and E. B. Brothers (CU) for the loan of specimens. I am further indebted to Ted Cavender for his thoughtful suggestions on this manuscript, and his support as my dissertation advisor, from which some material used in this paper was drawn.

APPENDIX I

TABLE 5

Female specimens used for egg diameter measurements

Name	N	Size (mm)	Catalog number	Locale	Date
Ericymba					
buccata	3	48.0-56.5	OSUM22010	OH, Ross Co, Salt Cr	20 May 1972
	2	48-54	OSUM45241	OH, Hocking Co, Laurel Twp, Pine Run	13 May 1959
	1	68	OSUM19592	OH, Logan Co, Bokes Cr Twp, Rush Cr	16 Apr 1963
Hybopsis					
amblops	3	50-53	OSUM28700	IND, Crawford Co, Whiskey Twp, Blue R	27 May 1942
Notemigonus					
crysoleucas	3	98-138	OSUM33845	OH, Ottawa Co, Put-in-Bay, L Erie	16 May 1955
Notropis					
amnis	1	47.5	OSUM28738	IND, Orange Co, French Twp, Lick Cr	28 May 1942
anogenus	2	38.0-38.5	OSUM20716	MI, Cheyboygan Co, Benton Twp	9 Jul 1970
ardens	3	48-52	OSUM2072	OH, Clark Co, Springfield Twp, Beaver Cr	28 May 1940
	3	61-65	OSUM42413	VA, Allegheny/Bath Co line, Cowpasture R	26 May 1972
atherinoides	3	78.5-82.5	OSUM24980	OH, Ottawa Co, Put-in-Bay, L Erie	26 Jun 1974
blennius	2	52-67	OSUM28784	IND, Daviess Co, Washington Twp, W Fk White R	2 Jun 1942
	3	61-71	OSUM28813	IND, Dubois Co, Harbison Twp, E Fk White R	3 Jun 1942
boops	3	54.9-62.2	OSUM39006	MO, Ripley Co, Fourche Cr	8 Jun 1976
buchanani	3	38.0-41.5	OSUM28590	IND, Lawrence Co, Shawsick Twp, E Fk White R	24 May 1942
	1	36	OSUM28872	IND, Dubois Co, Feroinand Twp, Huntly Cr	5 Jun 1942
chalybaeus	3	35-36	OSUM25485	IND, Steuben Co, Mill Gove Twp, Fawn R	19 Jul 1940
chlorocephalus	3	47-51	OSUM42467	NC, Mechlinburg Co, Catawba R, Irwin Cr	11 Apr 1968
	3	44-46	OSUM42512	NC, Mechlinburg Co, Catawba R, McAlpine Cr	1 Apr 1968
chrysocephalus	3	66.9-90.6	OSUM44731	MO, Ripley Co, Little Black R	9 May 1978
coccogenis	3	64.5-83.0	OSUM46772	NC, Swain Co, Little Tennesse R, Jct w Brush Cr	30 Apr 1980
cummingsae	2	46.0-46.5	OSUM42461	NC, Anson Co, Pee Dee R, Goulder's Cr	10 Apr 1968
dorsalis	3	50.5-52.0	OSUM14760	OH, Lorain Co, Pittsfield Twp, Black R	23 Jun 1964

TABLE 5 (continued)

Name	N	Size (mm)	Catalog number	Locale	Date
Notropis					
emiliae	3	41.5-43.0	OSUM45281	OH, Ottawa Co, L Erie	1955
greenei	3	50-60	OSUM38653	MO, Miller Co, Diane Cr	1 Jun 1976
heterodon	2	38.5-39.0	OSUM20717	MI, Cheyboygan Co, Benton Twp, Black R	9 Jul 1970
heterolepis	1	40.5	OSUM29243	IND, Porter Co, Boone Twp, Sandy Hook Ditch	17 Jun 1942
	3	43.8-48.5	OSUM48510	MO, Hickory Co, Little Pomme de Terre R	18 Apr 1979
hudsonius	2	72.0-72.2	OSUM21439	OH, Ottawa Co, Put-in-Bay, L Erie	23 Jun 1972
hypselopterus	1	37	OSUM12892	FL, Alachua Co, Sante Fe R	28 Apr 1941
leuciodus	3	53-58	OSUM46737	NC, Macon Co, Cullasaja R	1 May 1980
	1	61	OSUM46746	NC, Macon Co, Little Tennessee R	30 Apr 1980
nubilus	3	49.5-57.0	OSUM44470	MO, Camden-Hickory Co line, Little Niangua R	24 May 1979
	3	41-55	OSUM44849	MO, Ripley Co, Ripley Cr at Oxly	
	3	51-54	OSUM44930	MO, Texas Co, S prong Jacks Fk	11 May 1978
petersoni	2	58-65	OSUM42452	NC, Columbus Co, L Waccamaw	9 Apr 1968
photogenis	1	98	OSUM17955	OH, Logan Co, Pleasant Twp, Bokengehalas Cr	30 May 1964
	3	70.9-79.6	OSUM35359	OH, Logan Co, Jefferson Twp, Mad R	5 Apr 1973
	3	79.1-87.0	OSUM4961	OH, Columbiana Co, Middleton Twp, N Fk Beaver Cr	11 May 1972
	3	79.7-84.8	OSUM2124	OH, Logan Co, Monroe Twp, Mad R	30 May 1970
pilsbryi	3	69.5-86.0	OSUM44551	MO, Webster Co, James R	25 May 1979
procne	3	49-53	OSUM42408	VA, Chesterfield Co, Swift R	12 Jun 1972
pyrrhomelas	3	54.5-56.0	OSUM41804	NC, McDowell Co, Trib of Broad R at Rt 221	26 Jul 1978
rubellus	3	50-59	OSUM23042	OH, Pickaway Co, Salt Cr	No Date
	3	54-67	OSUM37563	PA, Cameron Co, Grove Twp, First Fk Sinnemahoning	No Date
	3	61.9-67.3	uncataloged	OH, Franklin Co, Big Darby Cr	No Date
N. sp. ("sawfin" shiner)	2	49.9-51.3	OSUM42097	VA, Washington Co, N Fk Holston R	2 Jul 1978
stilbius	1	52.5	CU21247	GA, Murray Co, Trib of Coosahattee R	12 Jun 1952
	3	59-65	CU21186	GA, Bartow Co, Trib of Etowah R	No Date
stramineus	2	54	OSUM15047	OH, Darke Co, Mud Cr	No Date
	3	50-54	OSUM20536	MI, Cheyboygan Co, Munro Twp, Douglas L	2 Jul 1970
	3	43.0-49.5	OSUM40100	MO, Callaway Co, Whetstone Cr	17 May 1977
telescopus	3	44-55	OSUM39116	MO, Vernon Co, W Br Fourche Cr	8 Jun 1976
	3	53-54	OSUM43463	KY, Pulaski Co, Fishing Cr	23 Apr 1978
	3	44-50	OSUM47782	MO, Ripley Co, Little Black R	9 May 1978
	3	62-71	OSUM46776	NC, Swain Co, Little Tennessee R	No Date
texanus	3	45-53	OSUM29357	IND, Newton Co, Beaver Twp	19 Jun 1942
umbratilis	3	49-52	OSUM17046	OH, Van Wert Co, Trib 27 Mile Cr	23 May 1970
	3	42.5-45.0	OSUM21558	OH, Ottawa Co, Portage R	29 Jun 1972
volucellus	2	52.5-53.0	OSUM25053	OH, Ottawa Co, Put-in-Bay, L Erie	19 Jun 1974
	3	46.5-52.0	OSUM24956	OH, Ottawa Co, Put-in-Bay, L Erie	19 Jun 1974
zonatus	1	78	OSUM39226	MO, Camden Co, Wet Glaize Cr	1 Jun 1976
Pimephales					
vigilax	3	43.0-49.5	OSUM28755	IND, Daviess Co, Elmore Twp, W Fk White R	1 Jun 1942

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